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A systems approach to animal communication

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Review

A systems approach to animal communication

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Abstract

Why animal communication displays are so complex and how they have evolved are active foci of research with a long and rich history. Progress towards an evolutionary analysis of signal complexity, however, has been constrained by a lack of hypotheses to explain similarities and/or differences in signalling systems across taxa. To address this, we advocate incorporating a systems approach into studies of animal communication—an approach that includes comprehensive experimental designs and data collection in combination with the implementation of systems concepts and tools. A systems approach evaluates overall display architecture, including how components interact to alter function, and how function varies in different states of the system. We provide a brief overview of the current state of the field, including a focus on select studies that highlight the dynamic nature of animal signalling. We then introduce core concepts from systems biology (redundancy, degeneracy, pluripotentiality, and modularity) and discuss their relationships with system properties (e.g. robustness, flexibility, evolvability). We translate systems concepts into an animal communication framework and accentuate their utility through a case study. Finally, we demonstrate how consideration of the system-level organization of animal communication poses new practical research questions that will aid our understanding of how and why animal displays are so complex.

Keywords: degeneracy, evolvability, modularity, multimodal, redundancy, robustness, behavior, ecology, evolution

1. Introduction

Animals often use elaborate signalling displays to communicate with conspecifics and heterospecifics across a variety of contexts and for a variety of reasons [1–3]. Important contributions have helped to categorize and formalize hypotheses of complex signal form and function [4–8], yet our understanding of how and why animals incorporate multiple distinct components within and across sensory modalities (multicomponent and multimodal signalling, respectively) remains in its infancy [9,10]. A critical missing piece for the study of animal communication is an evolutionary framework that enables an analysis and comparison of entire signalling systems—an approach that encompasses multiple signalling traits, the complex interactions among traits, and the structure-to-function relationships throughout. Specifically, there is a dearth of quantitative approaches aimed at assessing and interpreting potential similarities and differences in the design and function of signalling systems. The lack of a unified evolutionary framework and shared terminology constrains our ability to uncover broad patterns and to generate and test evolutionary hypotheses. To that end, we advocate applying a systems approach to the study of animal communication—an approach that considers the organization and structure/function relationships of the signalling system, including how components of the system can interact within and across contexts and how these interactions may change across time [11].

Current studies in animal communication continue to focus, predominantly, on (multiple) signal function(s) within a single condition. In contrast, a systems approach champions the quantification and assessment of the structure- to-function relationships within and across conditions (e.g. behavioral context, receiver identity, or physiological state, time). Systems theory and terminology are based upon structure/function relationships, whereas current hypotheses of complex signalling are based upon signal function, irrespective of its relationship with structure. By adopting a framework that is more aligned with systems biology, animal communication research can borrow from, and build on, a tremendous knowledge base and toolset aimed at understanding how and why systems function the way they do. Importantly, it will also provide a shared terminology and methodologies that can facilitate cross-system, cross-species comparisons of system design and function. Re-directing the field's research focus to include structure/function relationships across conditions will require both adjustments to our empirical approach (e.g. experimental design and data collection) as well as the purposeful integration and application of systems concepts, terminology, and analytical tools (and the potential development of new ones).

We lay out our proposal for the integration of a systems approach to animal communication by highlighting the current state of the field. We underscore the challenge of fitting complex empirical data within existing categorical frameworks by highlighting specific studies that demonstrate intersignal interactions and the dynamic nature of animal signalling systems (§2). We follow this with an introduction of systems concepts and associated terminology. We translate these concepts into an animal communication framework, and briefly discuss their evolutionary implications (§3). We then provide suggestions for how we might use systems thinking in animal communication research, including proposing tools and techniques for visualizing and comparing complex signalling architectures and interactions among components within the system (§4). We elucidate the utility of such an approach with a detailed case study of barn swallows. We end by discussing how new hypotheses that arise from considering animal signals as signal systems can advance animal communication research (§5).

2. Current state of the field

(a) Modelling multiple signals and functions

The study of animal communication has largely moved past the early univariate models that analyzed scenarios with one signaller, one receiver, and one signal serving one function [12,13]. It has importantly expanded its focus beyond selection for signal 'content', or information transfer, to a more inclusive view that acknowledges the importance of efficient signal transmission and the role of the receiver. Indeed, we now have good evidence for the existence of manipulative signals and signaller–receiver conflict [14,15]; and receivers are widely recognized as paramount in driving the evolution of signal form (reviewed in [4,16–20]). Empirical and conceptual progress in animal communication has even helped advance other areas of research focus, such as plant–insect interactions, as signalling theory has uncovered complex interactions between floral signals and their pollinator targets [21–23].

The first framework for classifying multimodal animal displays reflected a single function for a single signal [5]. Limitations of this approach, such as the difficulty of considering interactions between signal components and the possibility of individual signals having multiple functions, led to a suite of follow-up frameworks focused on intersignal interactions and potential sources of selection on signals [4,7,8,24]. The field has since been accruing multiple excellent case studies of complex signalling, including ground-dwelling spiders (reviewed in [25,26]), crustaceans (reviewed in [27]), anurans ([28], reviewed in [29]), insect pollinators (reviewed in [23,30]), birds [31,32], and primates [33,34], among others. Results from these studies and others have led to an appreciation that the function(s) of elements of communication displays are not fixed. Animal communication is multidimensional—it can encompass multiple strategies, multiple functions, multiple receivers, multiple components, and multiple sensory modalities [4,8,20]. We briefly elaborate on this with specific case studies.

(b) The dynamic nature of animal signalling

Animal displays can function differently across display compositions (system architecture) or timescales. Male *Schizocosa crassipes*, wolf spiders, for example, employ a multimodal (visual and vibratory) courtship display [35,36], the visual component of which includes dynamic waving of sexually dimorphic forelegs that possess conspicuous black brushes. Researchers have found that the function of the black brushes differs depending upon the presence versus absence of the multicomponent vibratory display. Specifically, females only respond to variation in brush size in the presence (versus absence) of the vibratory signal [37]. Thus, the relationship between the intensity of a signal component (visible brush size) and the behavioral response (likelihood to mate) is altered across display compositions (presence/absence of vibratory signal); and the vibratory signal interacts with a visual component (*sensu* [4]). Similar composition, environment, and receiver-dependent functions of complex signal components are found in other wolf spiders [38–42].

Functional interactions between signal components are also documented in the male túngara frogs, *Engystomops pustulosus,* which produce complex calls involving a whine and sometimes a chuck. Calls with both whines and chucks are more successful in attracting females and the temporal pattern of whines and chucks influences female responses [43–45]. The temporal coordination between the acoustic components and visual cues associated with calling (visible inflation of a vocal sac) also influences female responses [46]. Research on the squirrel treefrog, *Hyla squirella,* found similar cross-modal interactions [47]. Starnberger *et al.* [29] provide an excellent review of additional anuran signalling examples, including those in which temporal coordination among signal elements influences element function.

Individual receivers can vary in their perception and decision-making (reviewed in [19,48]) in an environment- or context-specific fashion, driven by past nutritional intake, hormone profiles, age, etc. Female round gobies, *Neogobius melanostomus,* for example, alter their response to uni- versus multimodal male stimuli across the breeding season [49], and the mate choice of female *Rabidosa rabida*, wolf spiders, is dependent upon both age and condition [50]. Even within a single display, female great bowerbirds are likely to perceive

Table 1. Redundancy, degeneracy, and pluripotentiality in animal communication: their translations into scenarios of complex signalling and their implications for understanding evolutionary patterns of animal communication systems.

Concept	Structure/Function	Communication scenario	System consequences	Evolutionary implications
redundant	same structure/ same independent function	repeated instances of a signal—repetition of a song or a display	increases robustness of a system	enables a system to maintain function in circumstances of loss (i.e. lack of transmission) of the element. Can relax selective pressure on duplicate structures and allow for functional or structural divergence
degenerate	different structures/ overlapping function	two different signals or signal components serving similar functions in some signalling contexts	increases robustness and can increase the functionality of the system	enhances capacity to respond to selection. Elements can react independently to selection; can diverge over evolutionary time to incorporate new functions while maintaining, or before losing, original function(s)
pluripotent	one structure/ multiple functions	the capacity of a particular signal or signal component to serve multiple functions in a display	increases efficiency and functional diversity of the system. Enables organization of coordinated responses to a signal	elements will likely be subject to multiple selective forces; any change in the signal will have multiple consequences across the system

colors differently at the beginning versus a minute into a male display bout [20].

The social context of a display can similarly influence not only the functional response of receivers, but also characteristics of the signal architecture itself. In the lance-tailed manakin, *Chiroxiphia lanceolata*, pairs of males perform more coordinated, predictably choreographed acrobatic displays in the presence versus absence of females [51,52]. Similar variation in signal form is seen in male wolf spider courtship displays in the presence versus absence of a female [53], whereas in the Australian field cricket, *Teleogryllus oceanicus*, the expression of male chemical signals is influenced by past social experience [54]. These case studies demonstrate how research efforts focused on relating individual signals to individual functions or individual receivers, at single time points and in single contexts, may overlook important interactions or variation among display components that are crucial to system function. As evidenced by these examples, more inclusive approaches to animal signalling are gaining momentum. We suggest that the impact of such approaches and resulting data will be truly significant if we can integrate them into a framework that can provide an avenue for cross-taxa/cross-study synthesis and hypothesis testing.

3. System properties of animal signalling

In addition to the impacts of systems approaches on experimental design, data collection, and analyses,we propose that studies of animal communication can benefit by adopting systems concepts such as *redundancy, degeneracy, pluripotentiality*, and *modularity* [55]—key organizational principles of complex biological as well as other (e.g. engineering) systems. These systems design principles influence vital aspects of system properties, such as the *robustness, flexibility* and, most relevant to biologically complex systems, its *evolvability*. Robustness, evolvability, and modularity are terms currently found in animal communication literature, though some more commonly than others. The term redundancy, though commonly employed, is regularly used imprecisely; and 'degeneracy' and 'pluripotentiality' have yet to make a predictable appearance. We discuss how these key systems design principles might translate into animal signalling to provide a richer view of signal–receiver function (table 1).

(a) Redundancy: Structurally identical components have identical functions

Elements in a system that are structurally identical and perform the same function independently are redundant [56–58] (table 1). This systems terminology refines the traditional use of this term in animal communication, which considers redundancy as a set of elements performing the same function, regardless of structure [5]. Refining the use of redundancy— to distinguish between signal elements with the same structure or different structures—impacts our view of robustness or resistance to changing conditions, and the evolutionary potential of the communication system (table 1). Repeating identical signal elements, for example, cannot confer as much robustness across signal environments and is subject to greater pleiotropic constraints on signal production compared with employing distinct signals for the same function. Additionally, the tradition of categorizing signal elements as 'redundant' based solely on function has arguably stifled progress towards understanding the prevalence and importance of true system redundancy (similar structure and function), such as the rich possible causes and implications of repeating song components

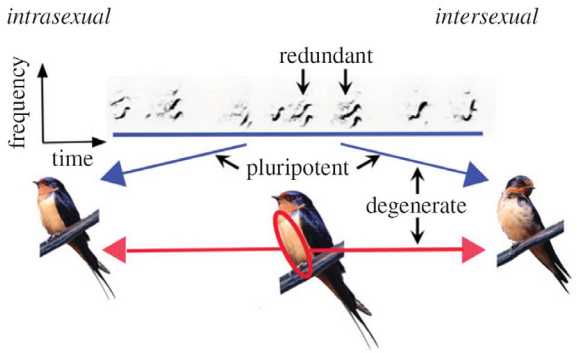

Figure 1. A heuristic example of the concepts and potential implementation of systems terminology based upon a recent study of animal communication [32]. Male barn swallows (centre), *Hirundo rustica erythrogaster*, communicate with conspecific males (left; *intrasexual*) and females (right; *intersexual*) using multimodal/multicomponent displays that encompass acoustic song (top; blue lines) and visual colour patches (red circle; red lines). Coloured lines with arrows indicate receivers (males and females) that respond to specific display components. *Redundancy* is seen in the repeated notes of the male's song. *Degeneracy* is seen in that two distinct display components (song and breast feather reflectance) overlap in function: territoriality (not highlighted) and female attraction [32]. *Pluripotentiality* is demonstrated by the dual function of song in both intra- and intersexual communication, and the similar dual function of breast feather color (not highlighted) [32].

(e.g. redundant notes; figure 1). Interestingly, despite its exclusion from many conceptual frameworks of complex signalling, research exploring 'consistency' in signalling (i.e. redundancy) is gaining momentum [59–62], and this growing research focus may benefit tremendously from the recognition that repetition and consistency might relate to both system redundancy and modularity (discussed below).

Redundancy provides a certain degree of robustness to a system[58]. If a redundant element is lost (e.g. a call is drowned out by environmental noise), repetition of the element can ensure that the signal still functions. In the king penguin, *Aptenodytes patagonicus*, for example, the repetition of similar syllables by adults is suggested to overcome the masking effects of the colony's background noise [63]. Such increased robustness, however, only occurs if the elements (syllables here) function independently; non-independent repeated elements do not fall as readily into the systems concept of redundancy and may not have the overall effect of increasing system robustness.

Redundancy changes the system's evolutionary potential [57,58]. This phenomenon is best illustrated by the classic example of gene duplication. Following duplication, selection on one gene copy might be relaxed, allowing mutations to accumulate that could, over time, result in the duplicated gene being exapted for a new function [56,64]. Similarly, redundant elements in displays have the potential to diverge, whereas at least one element maintains the original signal function [58]. A signal component could be co-opted, for example, from an initial function in mate attraction to a new function in competitor deterrence. Such an example would lead to pluripotentiality (same structure/multiple functions; table 1). Alternatively, though less likely, relaxed selection on a repeated signal component could enable change in component structure, resulting in system degeneracy (different structure/ overlapping function) if the now structurally distinct elements maintain a similar function (table 1) [56,57].

(b) Degeneracy: Structurally distinct components can have similar functions

Degenerate elements of a system differ structurally, but perform similar functions under certain conditions, although their functions may diverge across some environmental contexts or for some receivers (table 1 and figure 1) [56,57,64,65]. We have already mentioned the multimodal vibratory and visual sexual display of male *S. crassipes*, wolf spiders, [35,37,64,66] as an example of how total signal composition and interactions between signal elements can influence signal function; but this species also provides us with a good example of signal degeneracy. The integration of both vibratory and visual elements that can each subserve mate attraction reflects system degeneracy [37] and makes the display robust to changes in either light level or substrate properties. A similar example can be seen in the scent and color of floral signals. Under low-light conditions, the presence of scent increases a nectar-foraging bumblebee's accuracy to a target, whereas target accuracy is reduced with unscented targets [67]. Indeed, owing to degeneracy, multimodal signalling specifically has been argued to be more robust than multicomponent signalling [68].

Degeneracy increases robustness to a greater degree than redundancy and can also extend the functional range of the system (table 1). Because components of degenerate systems can potentially react to selection independently, unlike redundant signals and because function is shared across components, degeneracy can more readily facilitate the evolution of novel signalling phenotypes. Appreciating the degeneracy of signalling systems is likely to be illuminating for understanding broad patterns of signal divergence between species, and even repeated loss of sexually dimorphic signals [64,69,70].

(c) Pluripotentiality: Structurally similar components can have more than one function

When similar elements of a system can functionally diverge in diverse contexts, the system is said to exhibit pluripotentiality [57]. In animal signalling, many components may have distinct functions across contexts or with different receivers. For example, male snow buntings, *Plectrophenax nivalis*, display to other males with multiple visual plumage ornaments— breast feather and rectrices reflectance—one of which is also an attractive signal to females and is thus pluripotent [71]. An additional example can also be seen in the barn swallow, *Hirundo rustica erythrogaster*, in which both songs and breast feathers are signals to male competitors and to potential female mates [32] (figure 1). Whereas degeneracy increases system resilience in the face of environmental variation, pluripotentiality increases the functional diversity of a system across variation in environment or context (table 1).

Pluripotentiality can also introduce evolutionary constraints to the system, because signal components may be subject to a range of different selection pressures [72]; any evolved change could have multiple functional consequences. Accordingly, in the treefrog, *Dendropsophus ebraccatus*, shared production mechanisms across advertisement and aggressive calls are suggested to constrain signal structure owing to opposing selection pressures across social contexts [73]. Numerous studies support putative trade-offs between distinct signalling components within one context [74–78], but pluripotentiality could importantly lead to trade-offs within one display component across contexts [79].

(d) Modularity: a subset of components form tightly linked structural or functional clusters

Modularity refers to integrated groups of system elements that are distinct from other groups [55] (table 1). Integrated elements may be grouped, because either their structures or functions are linked. Structurally, display components might be grouped as a module owing to their tight covariance [32], or to their recurrence as a stereotyped unit in time or space [80]. Examples of structural modules in animal signalling might include particular notes, syllables, and phrases within a bird song, or different patches of color in a fish; these elements likely share developmental and physiological bases and thus are interrelated, yet are independent of other structures or elements. Incorporating analyses and concepts of modularity has already enhanced our understanding of the elaborate and lineage-specific diverse displays of *Parotia* birds of paradise [81,82].

Functional modularity, with its focus on receiver responses to groups of signal components, is an important counterpart to structural modularity. Identifying functional modules requires observations of receiver responses to multivariate variation in display structure. Functional modules may help explain why responses to some signal elements vary depending on the composition of a display (e.g. §3), and may even reflect the underlying neural architecture and processing of receivers. This hypothesis has not been fully examined in a neural–behavioral setting.

Distinguishing between structural versus functional modularity and understanding their relationship (a focus of research often termed phenotypic integration) will be vital to our understanding of the evolutionary dynamics of signalling systems, as the extent to which structural modules also act as functional modules has important evolutionary implications. Shared mechanisms and underlying genetic correlations that give rise to structural modules might constrain the evolution of a communication system if these developmentally integrated elements subserve diverse functions with divergent selection pressures. And yet the genetic architecture of signal traits may also be the result of selection to produce effective, coordinated signal elements by aligning patterns of structural and functional modularity [55].

4. Implementing a systems approach in animal communication

To implement a systems approach to the study of animal communication, we must expand our scope of data collection and identify, adapt, and apply existing tools and techniques to the structure and dynamics of animal signalling. We must strive to implement an overarching approach that is broadly applicable to variation in signalling contexts, taxonomic groups, and experimental design.

(a) Visualizing and characterizing signalling systems

Heuristic visual representations will be vital to the successful integration of a systems approach in animal communication, just as Partan & Marler's [5] original multimodal classification scheme was compelling and appealing in part owing to its intuitive and elegant visual representations. Towards a more comprehensive visualization of complex signal function, Smith & Evans [83] recently proposed a *geometric framework* in which they suggested representing responses to multimodal signals as surface plots in a three-dimensional space (e.g. figure 2). To illustrate this advance, consider the multimodal sexual displays of the wolf spider, *S. crassipes*, discussed in §2b where the efficacy of the foreleg brushes for mating success was greater in the presence versus absence of the vibratory signal [37]. By plotting responses to the signal components geometrically, we acquire quantitative details of signal effects and interactions (figure 2). A geometrical visualization is inherently extensible as additional behavioral responses or signal elements can be included as additional dimensions, enabling one to consider the full functional range of the signalling system.

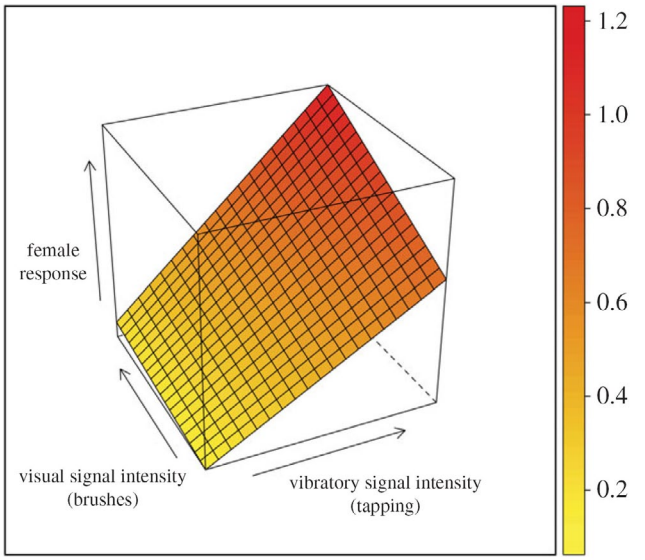

Figure 2. Building on the *geometric framework* of Smith & Evans [83], a heuristic graphical representation of a response surface highlighting interactions between vibratory and visual signal components of the courtship display of the wolf spider, *Schizocosa crassipes* [37]. Empirical data demonstrate that females respond to variation in brush size only in the presence, versus absence, of vibratory signalling [37]. This geometric visualization bears similarity to the multidimensional response surface methodology [e.g. 1], but rather than linking fitness to trait values to measure evolutionary responses to selection, here we plot behavioural responses as a function of trait (signal) values [84].

Signalling phenotype networks provide another very promising avenue for visualizing and quantifying signalling dynamics, due in part to the potential for generating comparable indices that reflect key system design features for cross-system, cross-taxa comparisons. Network thinking is commonly employed in studies addressing the evolution of integrated systems at the gene, protein, and ecological community level [85], but has only recently been applied in animal communication research [32]. Transforming complex signal structure into signal phenotype networks facilitates a view of the whole architecture of the signalling system, and similar approaches have become important tools in related fields such as phenotypic integration [86,87]. We highlight a case study that used phenotype network analyses to compare barn swallow signalling across two social conditions to demonstrate how such an approach can be more fully integrated into systems thinking and terminology.

(b) Barn swallow case study

Wilkins and co-workers took an important step towards systems thinking in their study of multimodal signalling in the North

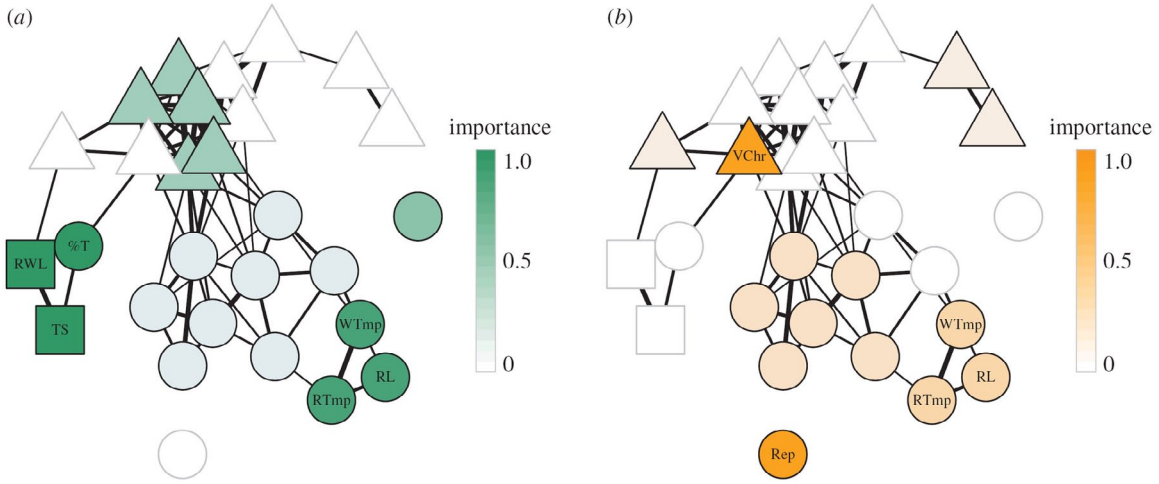

Figure 3. Signalling phenotype networks adapted from Wilkins *et al.* [32], illustrating the traits predicting (*a*) within-nest paternity and (*b*) internest distance in the barn swallow, *Hirundo rustica erythrogaster*. Triangles, colour variables; squares, morphological traits; and circles, song components. Lines connecting shapes represent Spearman's correlations and shape colours are graded by importance of rotated principal components (for details, see [32]). The best predictor of paternity (a surrogate for mate choice) was a factor with high loadings for wing length (RWL), tail feather length (TS), and per cent complex syllables (%T). The best predictor of internest distance (a surrogate for competition) was a factor with high loadings for the darkness of undertail contour feathers (VChr) and syllable repertoire size (Rep). The factor loading highly for a triad of song traits—warble tempo (WTmp), trill tempo (RTmp), and trill length (RL)—was the only strong predictor of both intra- and intersexual selection measures.

American barn swallow, *Hirundo rustica erythrogaster*. In the field, the research team collected a comprehensive array of phenotypic data from 50 males including measurements of 28 presumed display components (two wing and 12 color measurements; 14 measures of frequency, tempo, and repertoire per male) [32]. Field data were additionally collected to assess each male's success in intersexual communication (paternity analyses) and intrasexual communication (internest distance). Using a combination of principal component analyses and an information–theoretic approach, the research team was able to determine signal axes that best explained variation in paternity and internest distance. This innovative approach enabled them to assess both structure and function of display architecture within and across contexts (figure 3). Despite the limitation that some of their measured traits were not context-specific (i.e. not taken from a single individual at the time of displaying in a given context), the study nonetheless exemplifies an important advance towards an experimental systems approach to animal communication.

We used this dataset to demonstrate how integrating systems terminology and thinking into animal communication research can provide much more than a roadmap for how experimental studies can incorporate holistic, multicontextual approaches; it can aid in data interpretation, synthesis, and in elucidating future research avenues. We note at the onset that the authors' use of the term 'redundant' is 'degenerate' in systems terminology. Redundancy would pertain to consistency or repeatability of song structure as it relates to function (same structure/same function), which was not assessed in this study. We follow systems terminology throughout.

Upon constructing a signalling phenotype network, Wilkins *et al.* [32] calculated *network density*, the proportion of correlation coefficients that were significant, based on a bootstrapping procedure to remove non-robust correlations. This value is hypothesized to reflect system degeneracy (strong correlations suggest shared information and possibly shared function), allowing the team to directly compare inter- versus intrasexual signalling system degeneracy. Although they did not take their data this far, their results lead to concrete testable hypotheses regarding system robustness (e.g. intrasexual displays should be more robust to change given the slightly higher network density/degeneracy). The ability to quantify a value that encapsulates a hypothesized proxy of degeneracy opens up the possibility of directly and quantitatively comparing degeneracy across contexts (as shown here) and across taxa (not shown)— it provides a path towards assessing similarities and differences across signalling systems and determining how these might influence the evolution and function of display architecture.

The research team also sorted their display traits into predetermined categories (morphology, color, and song) and used assortativity coefficients to determine whether there were stronger correlations within the same trait types than across trait types. Indeed, they found that correlations within trait types were strong; morphological, acoustic, and color traits form separate clusters [32] (figure 3). These structural modules might reflect shared production mechanisms, pleiotropic effects, or shared function; all of which are testable hypotheses. Another intriguing module groups a measurement of song complexity with wing and tail streamer length measurements (figure 3*a*; %T, RWL, TS); a grouping that might suggest a functional interaction between components, correlated outcomes of early-life conditions and/or, shared hormonal/genetic underpinnings.

Visually, the generated phenotype networks exemplify the limitations of our traditional view of multimodal signal function. Across both contexts, highly correlated sets of signal components are grouped into structural modules (e.g. RL, RTmp, WTmp). The strong covariance of these modular components might suggest degeneracy (e.g. similar information content potentially reflecting similar function, with distinct structures). This pattern is reflective of a commonly tested hypothesis of complex signalling—content backup [4,88,89]. Simultaneously, distinct modules (or single nodes) within the system are demonstrated to share in their function through their predictability of behavioral outcomes. For example, within-nest paternity is

best predicted by two distinct modules (figure 3*a*—RL, RTmp, and WTmp and %T, TS, and RWL), whereas internest distance is similarly predicted by two distinct components (figure 3*b*; VChr and Rep) [32]. In these examples, despite the fact that the two modules/nodes share behavioral predictability, they do not covary and thus presumably do not share information content. This second scenario similarly suggests degeneracy (shared function with different structure) but without shared information (lack of covariance between modules/nodes). In contrast to the earlier pattern of content backup, this pattern can be directly related to another commonly tested hypothesis of complex signalling— multiple messages [4,88,89]. A systems approach importantly exposes the actuality that components within a single display can take on multiple functions within and across displays. It is also a useful example to caution against strict 'binning' of components or displays into discrete categories, even using the terminology we advocate here, as this can limit our understanding of animal signalling systems: 'multiple messages' and 'content backup' could simultaneously characterize parts of a complex signalling system.

The potential for signalling systems to convey multiple messages can similarly be explored by identifying the number of distinct structural modules across systems. For example, six uncorrelated modules are found to play a role in predicting male paternity (proxy for attractiveness to females), whereas only four modules are predictive of internest distances (proxy for effectiveness of territorial defences). An increased number of uncorrelated modules might suggest that intersexual communication has the potential to convey more information than intrasexual communication. Indeed, females may require more information from potential mates than males do for guiding agonistic encounters. This hypothesis could be tested more generally by comparing degeneracy of inter- versus intrasexual signalling systems across divergent taxa.

Although they did not use the term,Wilkins and co-workers also calculated an estimate of pluripotentiality—or the degree to which identical display components function across disparate contexts. Thirty-two per cent of their quantified display components predicted both paternity and internest distance [32]. Interestingly, among these traits is a module with different patterns of predictability across contexts—in the module composing song tempo: faster, shorter warbles and rattles predict male paternity, whereas slower, longer rattles predict internest distance. If this truly reflects opposing selection pressures of module components across contexts, it provides an excellent example of how pluripotentiality might constrain evolution for optimal signalling.

We have used this case study to demonstrate how shifting our focus from a narrow range of trait interactions (e.g. two traits or signalling modalities) to overall system architecture provides new insights. We demonstrate how one could use a signalling phenotype network approach to calculate and interpret degeneracy, modularity, and pluripotentiality; and how adopting systems terminology and analytical approaches can generate new hypotheses and open the door to original research directions.

(c) Outstanding challenges

Unlike many other fields of study, one of the most formidable practical challenges for animal signalling systems is the conceptual and analytical incorporation of the dynamic and transient nature of communication displays (for review of spatiotemporal dimensions of visual signalling, see [90]). How can we quantify, analyze, and compare systems characterized by components that are continuously variable in their expression and/ or perception? Temporal patterning, as a design feature (e.g. synchrony [91,92] versus asynchrony [93–95] of signal components), may hold significant explanatory power for the ubiquitous nature of multimodal animal signalling (e.g. sensory constraints, *sensu* [4]). We suspect that innovative analytical tools and techniques will best serve the purpose of quantifying and assessing temporal patterns of system design. We might borrow existing tools, for example, such as cyclic autocorrelation [96] to facilitate the measurement of relationships between signal components, or mutual information approaches to measure the extent to which one component/modality can be used to predict another. The relatively untapped aspect of temporal patterning in system design is likely to provide novel insights not only to animal communication, but also to systems biology more broadly.

5. Conclusion and future directions

The complex communicative displays that take place between many animals can be approached and studied as a system. This *system* can have multiple levels of analysis, from an individual signaller/receiver, to multiple signallers/receivers, to interacting species in a community [97]. Investigating how signal components function across contexts, including across signalling environments and variables receivers,will be essential for identifying systems design principles and properties; and clever experimental designs will remain vital to understanding signal interactions. We outline an innovative pathway for future research aimed at unifying and aligning studies of animal signalling systems with other scientific disciplines by adopting and adapting related concepts and tools. A system approach reorients readers from the current signal–function approach to an intuitive multidimensional/multifunctional approach that offers a more faithful evocation of animal communication.

Integrating systems thinking, experimental designs, terminology, and tools into animal communication research will provide a common language for cross-taxon comparisons of signal design. Thinking of animal signals as dynamic systems will (i) inspire testable evolutionary hypotheses addressing the patterns of system structure and function (e.g. degeneracy, modularity) and how systems respond to external factors (e.g. robustness, evolvability). It will (ii) lead to the development of innovative analytical tools and techniques integral for signalling system analyses and (iii) provide novel insights into cross-contextual selection pressure—e.g. intra- versus intersexual selection. A systems approach will also (iv) create avenues for comparing structure/function relationships within and across modalities to test the significance, or lack thereof, of modality-specific versus multimodal signalling. Finally, (v) a study of animal signals from a systems perspective will contribute to systems biology through its potential to assess and test systems design principles and properties in a comparative phylogenetic framework, enabling some of the first direct evolutionary tests of selection for systems design principles and properties.

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